

SILVICAL CHARACTERISTICS OF SUGAR MAPLE, ACER SACCHARUM, IN NORTHERN CAPE BRETON ISLAND

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A NUMBER OF FOREST TREE SPECIES of Canadian and Alleghanian affinity reach the limits of their natural ranges in northeastern Nova Scotia, failing to cross the Cabot Strait into nearby Newfoundland (Fernald, 1950; Rouleau, 1956; Little, 1971). Taxa reflecting this pattern of distribution include large-toothed aspen, *Populus grandidentata* Michaux; ¹ ironwood, *Ostrya virginiana* (Miller) K. Koch; beech, *Fagus grandifolia* Ehrh.; red oak, *Quercus rubra* L. var. *borealis* (Michaux f.) Farw.; American elm, *Ulmus americana* L.; sugar maple, *Acer saccharum* Marsh.; white ash, *Fraxinus americana* L.; and hemlock, *Tsuga canadensis* (L.) Carr. In northernmost Cape Breton Island this complex of elements is marked by wide differences between species in abundance and local distribution. For example, hemlock, large-toothed aspen, and ironwood are occasional and are possibly restricted to a narrow range of sites (Roland & Smith, 1969). Oak demonstrates minor, localized discontinuities in range and fluctuates widely in abundance. Sugar maple is abundant and distributed over a very broad range of sites, manifesting considerable morphological variability.

Studies have been initiated to obtain detailed information on regional distribution patterns, local habitat preferences, and site-density relations in red oak, sugar maple, ironwood, and hemlock in northern Cape Breton Island. Preliminary information bearing on the distribution and abundance of sugar maple in this area has been published previously (Greenidge, 1972). The present paper includes observations on habitat preferences, site-density relations, and morphological variability in sugar maple, with emphasis on patterns evident in the Grande Anse, Aspy, and Northeast Margaree watersheds (FIGURE 1).

BEDROCK GEOLOGY, PHYSICAL GEOGRAPHY, AND SOILS

The primary physiographic feature of northern Cape Breton Island is a massive, geologically complex plateau comprising Precambrian schists, gneisses, quartzites, and crystalline limestones, intruded by granites of pre-Carboniferous age. Contiguous and included lowland areas, as well as the outlying lower hills flanking the plateau, are underlain by Carboniferous sedimentary rocks (Nova Scotia Department of Mines, 1965).

From the sea, or from a vantage point on the tableland, the surface of the plateau appears relatively flat. In actual fact, however, the elevation of this surface ranges from approximately 1000 feet (305 m.) in the south

¹ Nomenclature follows Fernald (1950).



FIGURE 1. Map of Cape Breton Island.

to 1700 feet (518 m.) in the northern reaches of the island. Except to the southward, the flanks of the plateau either border the ocean or descend to a narrow coastal belt (FIGURE 1). There are strong indications of wide differences in the climate of upland versus lowland areas in northern Cape Breton. However, the absence of weather observation stations on the plateau surface renders valid quantitative comparisons impossible.

The tableland is being dissected by a number of short, swiftly flowing rivers and streams. Relief is considerable, and steep slopes form the approaches to the plateau, both from the sea and along the river courses. Instability is a common feature of many valley-side and seaward-facing slopes, and evidence of mass wasting is widespread. Slides and debris flows have occurred, and continue to occur frequently. In addition, accumulations of boulders, frequently of considerable extent, are common to many slopes.

Northern Cape Breton Island has been typed by Cann and MacDougall (1963) as rough mountain land characterized by steep slopes with ex-

cessively shallow, stony, weakly developed soils. The mapping of these soils was considered impractical by Cann and MacDougall. The bottomland soils of the sample areas have been mapped as deriving from fine-textured till, from medium-textured till with admixtures of alluvium, and from coarse-textured fluvial materials.

PLEISTOCENE AND POST-PLEISTOCENE HISTORY

The glacial and postglacial history of northern Cape Breton Island is incompletely known. Evidence of extensive lowland glaciation has recently been reviewed by Grant (1971a; 1971b; 1972) and by Prest and Grant (1969). However, the surficial history of the upland surfaces remains obscure.

Prest and Grant (1969), while acknowledging the abundance of constructional glacial features in lowland Cape Breton, invite attention to the relative paucity of ice flow features on the highlands. Plateau surface configuration, together with the occurrence of areas of gross and rotten rock resembling preglacial saprolite, led Newman (1971) to conclude that glacial erosion of the highlands was superficial. The filling and partial filling by till of deeply incised, V-shaped stream valleys, and the shallow depths of postglacial notching of bedrock-floored valleys have prompted Newman (1971) to suggest that the bedrock topography reflects a pre-Wisconsin, perhaps pre-Pleistocene landscape. However, Newman also presents evidence of topographic modification of pre-existing stream valleys, noting the presence of over-steepening in valley profiles, truncation of spurs, discordant stream junctures, and changes in valley form associated with changes in valley orientation.

Several sets of striae have been observed on the upland surface. Consistency in orientation of these striae has led Newman (1971) to conclude that northern Cape Breton was crossed by southeastward moving ice during the "classical" Wisconsin substage.

A rather different conception of the glacial history of the Cape Breton highlands has been developed by Prest and Grant (1969). In their view, the concept of Laurentide ice moving over the highlands is unacceptable. The available erosional and depositional evidence has prompted them to predicate the existence of a highland ice cap which was neither extensive nor active. In a later paper, Grant (1971b) developed this thesis further, interpreting crag and tail features on eastern and western slopes of the plateau as evidence of the existence of a "full-fledged" ice cap on the northern plateau.

In a more recent assessment, Grant (1975) presents a modified appreciation of his original thesis. A more complex sequence is envisaged, involving over-riding of the highlands by Laurentide Ice and subsequent occupation of the highlands and central plateau region by a local ice cap flowing radially to the sea. Age relations between Laurentide Ice and flow from the previously postulated lowland ice mass to the south have not been clarified (Grant, 1975).

On botanical and geological grounds, Fernald (1925) suggested that several upland surfaces (including the Cape Breton Plateau) in the Gulf of St. Lawrence region may have escaped glaciation. However, Livingstone and Estes (1967) conclude that the results of zoogeographic studies do not support "the botanical suggestion of a long, ice free history for the Cape Breton Plateau." Although Livingstone and Estes (1967) contend that appeal must be made to glaciation to explain the presence of numerous lakes on the plateau surface, they point out that the age of the lakes is unknown. Consequently, if formed early in the Wisconsin, the plateau surface might subsequently have served as a refugium for plants and animals.

Quaternary deposits bearing buried organic materials have been recognized and mapped in central and northern Cape Breton Island. Mott and Prest (1967) have discussed three such deposits, the ages of which range from $>38,270$ to $>51,000$ years. Deposition is thought to have occurred in preclassical Wisconsin time, and the deposits are related to an early Wisconsin interstadial interval. Newman (1971) has described a younger till with included organic materials which have been radiocarbon dated and accorded an age of the order of 21,000 years. Grant (1975) has reported four sub-till peat and wood occurrences from eastern Cape Breton Island which have been accorded ages of the order of 10,000 years. These deposits have been interpreted by Grant (1975) as indicative of a "significant readvance of the lowland ice mass ca. 10,000 years ago."

In the matter of deglaciation, Livingstone and Estes (1967) suggest that organic sedimentation on the Cape Breton Plateau was initiated about 9000 years ago. These authors postulate that prior to that time, an open tundra with scattered conifers and poplar characterized the upland surface, and that subsequent to the onset of organic sedimentation, a closed fir forest similar to the contemporary forests of parts of Nova Scotia has constituted the principal vegetation type. Prest's (1969) appreciation of the patterns of retreat of Wisconsin and recent ice indicates that the ice margin had reached the area of the Cape Breton Plateau about 12,500 years B.P.

FORESTS

The forests of northern Cape Breton Island have been discussed recently by Loucks (1962) and Rowe (1972). Consequently, only a brief, generalized description is included here.

Considerable variation in cover type is apparent in the forests of the sample areas. Bottomlands and lower slopes, together with the middle sections of stabilized, valley-side slopes, support virgin or disturbed, hardwood or mixed-wood forests differing widely in age, composition, and history. Stabilized, upper-valley-side slopes and the gentle, peripheral slopes of the plateau are characterized by a structurally variable, transitional forest comprising needle-leaved and broad-leaved elements in diverse mixtures

with a tendency toward regional differentiation. In the Aspy and Grande Anse watersheds, these upper-slope forests comprise mixed woods and mixed wood-softwood transitions, whereas in the Northeast Margaree the percentage of broad-leaved elements is higher.

On occasion, extensive areas of mid-slope and crest-slope segments of steep, valley-side slopes may support an irregular, unthrifty forest composed of white spruce, *Picea glauca* (Moench) Voss; and balsam fir, *Abies balsamea* (L.) Miller. Pronounced steepness, outcrops of bed rock, and a coarse, surficial mantle are commonly associated with this cover type.

The slightly rolling surface of the tableland supports a needle-leaved forest composed largely of balsam fir, with admixtures of white spruce; black spruce, *Picea mariana* (Miller) BSP.; larch, *Larix laricina* (Du Roi) K. Koch; and white birch, *Betula papyrifera* Marsh. The continuity of this plateau forest is broken by bogs and barrens of wide occurrence and considerable extent, by areas of wind-throw, and, in the south-central region, by recent clear-cutting operations.

METHODS

Field studies were concentrated in the lower and middle reaches of the North Aspy and Grande Anse rivers, and in the middle and upper Northeast Margaree (FIGURE 1). Sample plots were utilized to obtain information on occurrence and density on sites of limited topographic diversity, i.e., upland surfaces, terraces, and bottomlands. Conversely, distribution and density on topographically well-defined sites were investigated by means of cruise lines. Transects were disposed across contours on straight slopes in interfluvial areas, and along the axes of spurs, stream-hollows, and valley-heads.

Morphological variation in sugar maple was investigated by means of stem-analysis trees and via diameter-height-age relations.

OBSERVATIONS

SITE-DENSITY RELATIONS

Bottomlands and foot-slopes. TABLE 1 includes data reflecting the occurrence and abundance of sugar maple in forested bottomland sites in northern Cape Breton Island. Valley-bottoms and foot-slopes² of the Grande Anse and North Aspy watersheds frequently support old-growth, broad-leaved forests in which the density (trees per acre) and basal area (sq. ft. per acre) of sugar maple are high, with the species represented over virtually the entire range of diameters encountered in the stands. The tolerance of sugar maple in these forests is expressed in its high percentage representation in the smaller diameter size classes, while its longevity and competitive potential are reflected in its continued high percentage occurrence in the middle and larger diameter size classes.

² Slope terminology follows Leopold, Wolman, & Miller (1964).

TABLE 1. Diameter-density relations for sugar maple in old-growth, bottomland forests in northern Cape Breton Island.

DBH (in.)	GRANDE ANSE RIVER		NORTH ASPY RIVER		NORTHEAST MARGAREE RIVER	
	Number of trees		Number of trees		Number of trees	
	All species	Sugar maple	All species	Sugar maple	All species	Sugar maple
4	39	22	63	19	73	24
5	20	18	34	9	44	23
6	15	12	25	8	25	9
7	22	15	22	6	21	16
8	19	15	25	10	23	19
9	16	12	18	10	15	12
10	15	13	17	10	18	16
11	11	9	14	7	14	14
12	15	12	13	5	15	14
13	17	13	13	8	9	9
14	9	3	12	9	5	3
15	12	9	9	5	19	17
16	8	5	9	4	10	9
17	11	9	7	6	4	4
18	9	2	5	3	6	5
19	8	5	7	6	5	5
20	7	3	3	3	2	1
21	8	3	7	4	5	4
22	3	1	2	—	4	2
23	2	1	2	1	2	2
24	5	1	5	3	2	2
25	—	—			1	1
26	3	—				
27	2	1				
28	4	—				
29	2	2			1	—
30	2	—				
31	3	—			1	1
32	2					
33	1					
34	1					
35	1					
36	—					
37	1					
38					1	—
Area (acres)	1.6		1.53		1.65	
Total trees	293	186	312	136	325	211
Trees per acre	183	116	204	89	197	128
Percentage	100	63	100	44	100	65
Basal area per acre	206 ft. ²	88 ft. ²	130 ft. ²	73 ft. ²	125 ft. ²	97 ft. ²
Percent	100	43	100	56	100	77

Despite proximity to the northeastern limits of the range of the species, individual sugar maples in these protected, bottomland stands reach impressive size and age. A large tree in the Grande Anse Valley, apparently felled in 1956, and displaying measurable diameter growth at the time of felling, was approximately 230 years of age at stump height. In a sample of six sugar maples measured in the Grande Anse Valley in 1967, diameters at breast height ranged from 14 to 34 inches (36–86 cm.), and heights, determined with the aid of an Abney level, varied from 79 to approximately 100 feet (24–30.5 m.). In the North Aspy and Northeast Margaree stands, canopy sugar maples vary from 75 to 95 feet in height (22.9–28.9 m.).

Canopy associates of sugar maple in old-growth, bottomland stands include yellow birch, *Betula lutea* Michaux f.; red maple, *Acer rubrum* L.; red oak; white ash, *Fraxinus americana* L.; white spruce, and balsam fir. Occasional balsam poplar, *Populus balsamifera* L., hemlock, and white birch occur in the canopy of the North Aspy stands.

With regard to regeneration, Clattenburg (1962) has estimated that in the Grande Anse stands, the number of woody plants per acre which exceed one foot (30 cm.) in height but are less than 3.5 inches (9 cm.) in diameter at breast height approximates 7915 stems. Included in this total are approximately 6000 sugar maple saplings. Clattenburg's estimate of the number of woody plants per acre under one foot in height is approximately 104,000, of which 94,000 are estimated to be sugar maple seedlings. Regeneration of sugar maple is less prolific in the North Aspy and Northeast Margaree stands.

Higher terraces and benches. The abundance of sugar maple on benches and terraces in northern Cape Breton Island varies widely. In undisturbed stands the species is commonly abundant on the treads of both strath and alluvial forms. However, very low densities of sugar maple are encountered in disturbed stands on the coarse-textured fans and fluvial deposits of the Northeast Margaree River. Again, in a given reach characterized by the presence of two or more terrace levels developed in fluvial materials, the density of sugar maple may be considerably higher on the lower or lowermost tread than at higher elevations. Density relations for sugar maple on strath and alluvial terraces are presented in TABLE 2.

It is clear that sugar maple may constitute a primary element of forests occupying both strath and alluvial terraces. In the North Aspy stands, the density and basal area of sugar maple approach levels characteristic of nearby bottomland forests. Individual sugar maples reach heights of 90 feet (27.4 m.) in these terrace forests, with the species distributed over virtually the entire range of diameters included in the plot tally. The diameter-class distribution of sugar maple suggests the continued primacy of the species on these surfaces. Canopy associates of sugar maple in the North Aspy terrace stands include red oak, red maple, yellow birch, and balsam fir. Regeneration of sugar maple is good in the North Aspy stands; it is not as good in the Northeast Margaree area.

TABLE 2. Diameter-density relations for sugar maple in undisturbed stands on strath and alluvial terraces.

DBH (in.)	NORTH ASPY RIVER (STRATH)		NORTHEAST MARGAREE RIVER (ALLUVIAL)	
	All species	Sugar maple	All species	Sugar maple
4	37	12	152	105
5	21	5	133	91
6	13	5	132	93
7	8	4	104	80
8	12	4	76	53
9	10	3	71	52
10	7	7	57	39
11	8	4	41	33
12	11	6	31	21
13	10	7	34	23
14	4	2	18	13
15	9	6	24	13
16	5	2	30	12
17	10	5	22	16
18	4	3	15	12
19	5	3	16	9
20	4	2	11	5
21	1	—	18	13
22	4	2	10	8
23	2	1	12	9
24	2	1	3	2
25	—	—	7	3
26	—	—	3	2
27	—	—	2	2
28	1	1	2	1
29			3	1
30			2	
31				
32			1	1
33			1	
40			1	
Area (acres)	1.2		6.2	
Total trees	188	85	1032	712
Trees per acre	157	71	166	115
Percentage	100	45	100	69
Basal area per acre	116 ft. ²	63 ft. ²	109 ft. ²	70 ft. ²
Percentage	100	54	100	64

Valley-side slopes and allied forms. Wide variations in density characterize the distribution of sugar maple on hill-slopes in northern Cape Breton. On straight slopes in interfluvial areas, sugar maple varies in importance from a primary species to a minor element of the canopy. Well-defined differences in density are evident between slopes and between segments of the same slope within a modest altitudinal interval. TABLE 3 includes data reflecting abundance levels in sugar maple in transects extending from valley-bottoms to the plateau surface.

Reference to TABLE 3 indicates that in stream-hollows and valley-heads, where contours are disposed in a concave-outward pattern, the density of sugar maple is commonly high. Alternatively, on convex-outward forms (spurs), the density of the species reflects greater variability. On steep, narrow spurs lying between intersecting streams, the species frequently is virtually absent. However, on similar features of considerable lateral extent, bordered on either flank by subparallel drainage channels, the density of sugar maple occasionally may be moderately high (TABLE 3).

Data on variability in density of sugar maple with change in topographic setting, taken from a previous paper (Greenidge, 1972), are shown in TABLE 3. A transect was oriented parallel to but slightly down-slope from the axis of a steep, narrow spur, across a shoulder, then into a stream-hollow crossing this feature diagonally. Emerging from the hollow, the traverse passed upward across a short, steep, straight slope, then on to the gentle peripheral slopes of the plateau surface.

The data indicate that sugar maple is absent to infrequent on the axis of the spur. The species increases in abundance on approaching the shoulder, and reaches maximum density in the stream-hollow. Beyond the stream-hollow the density of the species again decreases on the steep valley-side slope, declining steadily toward the plateau surface.

Plateau-surface. In the middle and upper reaches of the Northeast Margaree, the break in slope separating the steep valley-sides from the gentle approaches to the upland surface occurs at elevations of the order of 1100 to 1200 feet (335–366 m.) above sea level. This alteration in slope is commonly accompanied by striking changes in forest form and composition. Immediately above the break in slope, but below the elevation limit of the range of sugar maple (ca. 1300 feet (396 m.) in the Margaree watershed), the gently rising upland surface supports an open, parklike, mixed-wood forest composed of short-stemmed individuals of very poor form. Species represented in the canopy of these stands include yellow birch, white birch, sugar maple, red maple, balsam fir, and white spruce. In these virtually undisturbed, peripheral, upland forests, the percentage of sugar maple in the overstory may be moderately high, with the species occurring over a considerable segment of the range of diameters represented (TABLE 4).

TABLE 3. Diameter-density relations in sugar maple on valley-side slopes and allied topographic forms.

WATERSHED LOCATION	MARGAREE		GRAND ANSE		ASPY		ASPY		MARGAREE		MARGAREE		
	Valley-side slope		Valley-side slope		Valley-side slope		Broad spur		Stream hollow		Variable		
Density	Trees per 0.1 acre		Trees per 0.1 acre		Trees per 0.1 acre		Trees per 0.1 acre		Trees per 0.1 acre		Land form	Trees per 0.1 acre	
	All species	Sugar maple	All species	Sugar maple	All species	Sugar maple	All species	Sugar maple	All species	Sugar maple		All species	Sugar maple
Distance plot center from datum (chains)													
1	35	12	12	8	28	2	36	5	38	22	Spur	29	4
3	42	11	18	12	31	3	47	7					
5	39	10	18	14	30	1	22	10	48	34	Spur	23	0
7	56	9	18	18	30	1	16	5					
9	49	8	16	16	38	0	21	6	32	26	Spur	21	0
11	51	11	8	8	47	2	18	7					
13	58	5	24	16	46	0	22	12	36	23	Spur	23	3
15	22	6	20	10	50	0	27	4					
17	23	1	12	6	(Outcrop)		25	5	33	3	Spur	28	0
19	48	5	20	16	32	8	22	8					
21	42	8	18	16	18	5	34	7	24	17	Spur	39	3
23	44	4	18	8	13	6	17	9					
25	54	8	24	6	21	18	19	17	20	18	Spur	47	0
27	34	7	18	2	22	22	16	14					
29	23	15	22	0	20	7	12	9	37	6	Shoulder	34	3
31	15	7	50	0	37	0	12	3					
33	16	0	12	0	20	0	21	3	46	—	Stream hollow	23	4
35	35	0	40	0	32	0	14	1			"	18	11
37			18	0			23	0					
39							27	0			Straight slope	37	3
41											Upland surface	11	1
43											Upland surface	35	0
45													
47													
49													
51													

TABLE 4. Diameter-density relations for sugar maple on the plateau surface.

DBH (in.)	PERIPHERY OF PLATEAU SURFACE		NEAR LIMIT OF RANGE	
	All species	Sugar maple	All species	Sugar maple
4	113	84	44	3
5	74	49	21	3
6	74	52	30	5
7	41	31	21	6
8	62	45	12	1
9	57	47	22	5
10	54	42	15	4
11	43	35	21	4
12	35	25	16	3
13	17	13	4	0
14	20	15	9	0
15	19	10	7	2
16	8	7	4	0
17	5	1	4	0
18	4	2	2	1
19	6	0	1	0
20	2	0	3	0
21	—	—	5	0
22	2	0	—	—
23	2	0	1	0
24	2	1	4	0
25	1	0	—	—
26			2	0
27				
28				
29	1			
30	1			
31	1			
Area (acres)	2.4		1.1	
Total trees	644	459	248	37
Trees per acre	268	191	225	34
Percentage	100	71	100	15

However, as one approaches the altitudinal limit of the range of sugar maple in the Northeast Margaree region, the parklike quality of the upland stands becomes less evident, and there is a pronounced decrease in the density of sugar maple with a concomitant increase in the percentage of balsam fir. The actual "farthest-on" position of sugar maple comprises a zone of diffusely scattered trees. On the apparent limit of the range of the species, individual sugar maple stems show no evidence of depauperate habit, occurring rather as codominant members of the overstory, albeit of very poor form.

In the Grande Anse and North Aspy rivers, the break in slope separating

TABLE 5. Diameter-height relations in sugar maple on a uniform site (valley-side and hollow of a small stream) over a 700-foot vertical interval.

APPROX. ELEVATION (FT.)	DBH (IN.)	HEIGHT (FT.)
300	5	47
	7	64
	13	81
442	9	72
	12	74
537	7	56
	8	60
631	7	55
	9	57
	11	73
726	9	48
	11	57
820	8	45
	9	34
915	9	36
	12	41
1010	6	31
	11	33

the upland surface from the steep, valley-side slopes occurs at elevations of the order of 1350 to 1400 feet (412–427 m.). Sugar maple commonly attains the altitudinal limits of its range on the valley-side slopes and is not a frequent constituent of the plateau surface forests of these regions.

MORPHOLOGICAL VARIABILITY

Well-defined differences in height growth and form distinguish sugar maples on upland from bottomland sites in northern Cape Breton Island. As noted previously, sugar maples growing in the valley-bottoms of the Margaree and other streams may approach 100 feet (30.5 m.) in height. In contrast, on nearby upland sites some 1000 feet (305 m.) higher in elevation, sugar maples of considerable age (125 years and older) attain heights of 45 feet (13.7 m.) and less. Height-diameter relations for sugar maple on a relatively uniform site (valley-side and hollow of a small stream) extending over a 700-foot (213 m.) interval in the Margaree region are illustrated in TABLE 5.

Differences in the absolute size of trees from upland as opposed to bottomland sites are accompanied by equally well-marked differences in overall form. Codominant sugar maple stems in the diameter range of 7 to 11 inches (18–28 cm.) at breast height growing on good sites (i.e., protected, moist bottomlands) reach heights of the order of 60 to 80

feet (18.3–24.4 m.). Under these circumstances, length of bole per inch diameter at breast height ranges from 8.6 feet (2.6 m.) in the smaller (7 inch) size classes to 7.3 feet (2.2 m.) in the larger diameters. However, codominant trees within the same diameter range situated on crest slopes and the plateau surface fall between 35 feet (10.7 m.) and 50 feet (15.2 m.) in height. Thus, for codominant trees of equal diameter, length of bole per inch diameter at breast height in stems from protected bottom-lands is approximately 60 percent greater than in material from the plateau surface. In terms of height and height-diameter relations, codominant sugar maples in protected valley-bottoms are taller and of considerably better form than individuals of the same diameter growing on upland sites. Patterns of height growth for codominant sugar maples located respectively on a protected lower slope, on an exposed mid-slope, and on the plateau surface are illustrated in FIGURE 2.

DISCUSSION AND SUMMARY

The landscape of northern Cape Breton Island is marked by considerable physiographic diversity. Topographic variability, together with differences in surficial geology and land surface history, contributes to the existence of a wide spectrum of habitats available to plants. As indicated

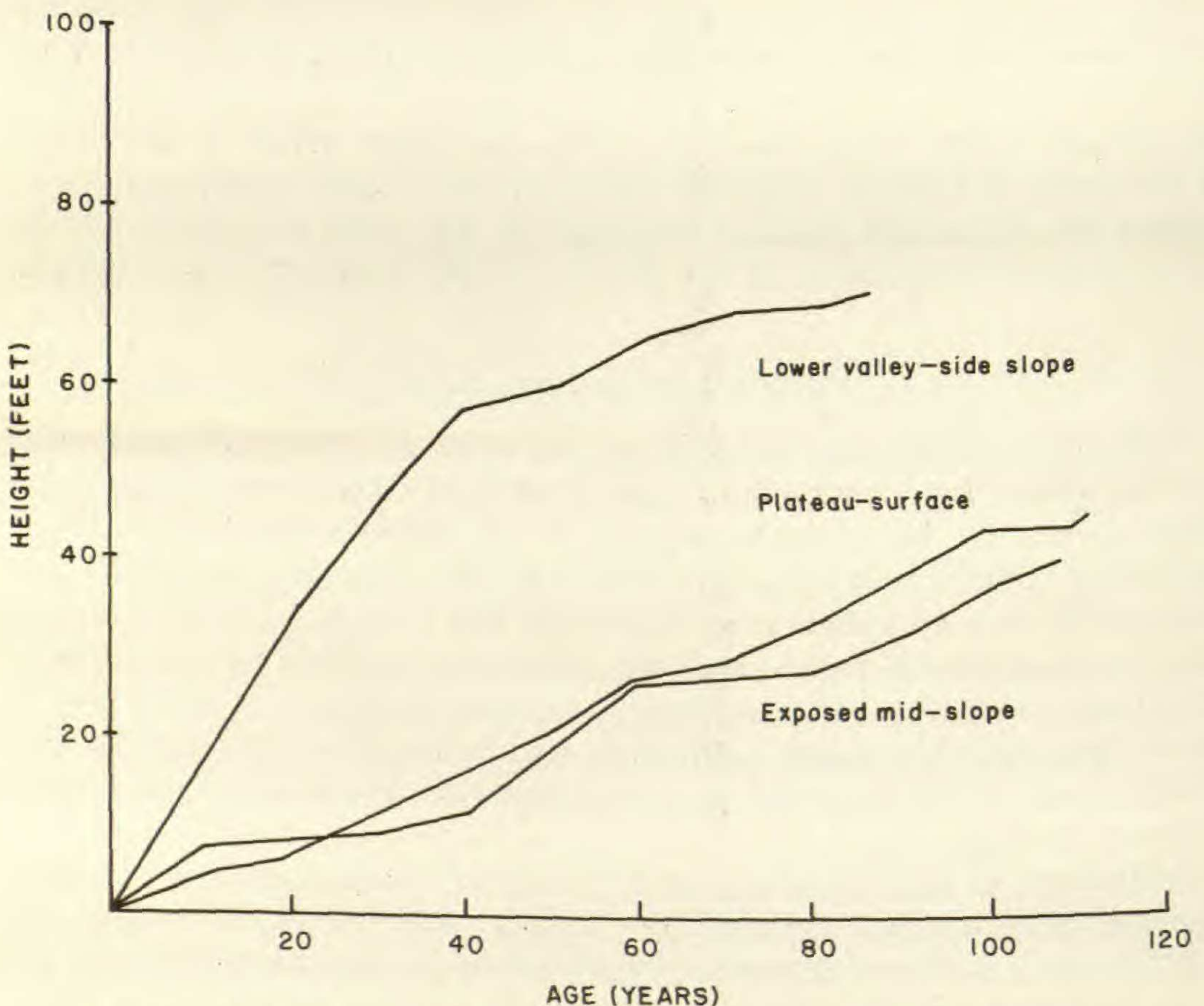


FIGURE 2. Height growth in codominant sugar maples on different sites.

in the foregoing tables, sugar maple, manifesting wide ecological amplitude, is distributed over a considerable segment of the available range of sites.

The species is very common on bottomlands and foot-slopes. On somewhat drier, low-level surfaces such as fans and terraces, the abundance of sugar maple ranges from low to high. Density commonly is high in undisturbed stands occupying the treads of strath terraces and benches. Conversely, species representation is variable but commonly low on the disturbed alluvial fans and terraces of the Northeast Margaree River.

On mid-slopes and crest-slopes in interfluvial areas, sugar maple varies widely in density, ranging from a few stems to a high percentage representation per acre. On moist sites at medium and higher elevations (stream-hollows and valley-heads), the density of sugar maple commonly is high and often appreciably greater than on nearby valley-side slopes. On spurs the density of sugar maple is extremely variable, with medium high concentrations of the species often occurring on features of wide lateral extent, and very low densities being encountered on steep, narrow forms.

The density of sugar maple declines rapidly on approaching the altitudinal limits of the range of the species. The "farthest-on" position may be encountered either on the gentle slopes of the plateau surface or on the uppermost segments of steep, valley-side slopes. The apparent limit of sugar maple in northern Cape Breton Island comprises a zone of diffusely scattered trees, with individuals of the species continuing to form part of the forest canopy.

Fowells (1965) has examined the habitat preferences of sugar maple, noting that the species prospers on moist, well-drained sites, and that yield and quality increase with improvement in soil-moisture conditions. Site-density relations in northern Cape Breton Island support the suggestion of a coincidence between the abundance of sugar maple and soil-moisture regimes. In northern Cape Breton, sugar maple is distributed over a broad range of sites and reflects a tendency toward high densities on sites where runoff and seepage water are concentrated and less quickly dispersed. High densities also occur on fresh sites such as stream-hollows, where contours assume a concave-outward configuration, indicating a zone of possible concentration of moisture in the ground. Moderately high densities are to be found on strath terraces and the peripheral reaches of flattish upland surfaces where runoff and seepage water are less quickly dispersed. Low densities of sugar maple are found on sites marked by rapid drainage, such as coarse-textured fans, narrow spurs, and steep mid-slopes and crest-slopes.

A particularly striking aspect of the geography of sugar maple in northern Cape Breton Island is the deterioration in height and form which characterizes the species in passing from protected, moist bottomlands to exposed crest-slopes and the plateau surface. Canopy sugar maples, in a vertical interval of 1000 feet (305 m.) or less, may reflect a reduction in relative height of 50 per cent or more over the foregoing gradient. Accordingly, in the forests of peripheral reaches of the tableland, sugar maple, while continuing as an overstory species, characteristically demon-

strates much reduced height and very poor form on the individual tree level.

A comparison of the behavior of sugar maple on the limits of its range in northern Cape Breton Island with that of the species in like circumstances elsewhere reveals both similarities and differences. Braun (1950) and Dansereau (1943) have commented on the confinement of sugar maple to summits, ridge-tops, and well-drained slopes in northern sections of the hemlock, white pine, northern hardwoods forest of Ontario and southwestern Quebec. Cater (1961) has observed that, on the limits of its range in northwestern New Brunswick, sugar maple is abundant on, and apparently restricted to, hilltops and upper slopes, but is absent from lower slopes and bottomlands. Dansereau (1944) has pointed out that, in the Gaspé Peninsula of Quebec, sugar maple is restricted to gentle slopes at elevations of approximately 200 to 600 feet (61–183 m.) in the interior valleys and on outlying hills of the Shikshok escarpment. Alternatively, Bormann *et al.* (1970) and Siccama (1974), working in the White Mountains of central New Hampshire and the Green Mountains of Vermont, respectively, report distribution and behavior patterns in sugar maple on the limits of its range in those areas which appear to resemble the patterns reflected by the species in northern Cape Breton Island.

Notable features of the geography of sugar maple in close proximity to the limit of its range in northern Cape Breton Island include broad ecological amplitude, relatively high density of stocking and, in protected bottomland sites, impressive stature and vigor on the individual tree level. Salient aspects of the distribution pattern of the species include restriction of the range to a vertical interval of the order of 1000 feet (305 m.) and abrupt altitudinal truncation of the range. Also noteworthy is the status of individual sugar maples on the periphery of the range. The limiting trees are almost invariably codominant members of the overstory, approaching or equaling in height and diameter the dimensions of trees of other species represented in the canopy. Despite the reduction in size and deterioration in form of range-limit trees in comparison with individuals of similar diameters in nearby bottomland sites, there is no suggestion of a decline in stature to a depauperate habit over the elevation gradient, or of a marked decrease in vigor upon approaching the limit of the range of the species.

The factors which control or which have contributed to the present pattern of distribution of sugar maple in northern Cape Breton Island are not clearly defined. As noted in a previous paper (Greenidge, 1972), the present altitudinal limit does not appear to be linked to topographic or edaphic changes or discontinuities. Putative climatic effects are suggested by unthriftiness in sugar maple regeneration at elevations slightly exceeding the altitudinal limits of nearby canopy trees, and by differences in the altitudinal limit on seaward-facing versus inland sites (Greenidge, 1972). Likewise, competition may be a factor restricting the spread of sugar maple at higher elevations in the region. Similarly, historical fac-

tors, particularly Pleistocene and post-Pleistocene events, may be of great significance to the contemporary patterns of distribution of sugar maple in the area.

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DEPARTMENT OF BIOLOGY

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A REVISION OF THE PAPUASIAN SPECIES OF
ACMENA (MYRTACEAE)

T. G. HARTLEY AND L. A. CRAVEN

IN THE MOST RECENT taxonomic work dealing with the Papuan species of *Acmena* DC. (Merrill & Perry, 1938 & 1942), six species were recognized for the area: four endemic, *A. dielsii* Merr. & Perry, *A. dispansa* (Ridley) Merr. & Perry, *A. laevifolia* (Ridley) Merr. & Perry, and *A. polyantha* (Lauterb. & K. Schum.) Merr. & Perry; one Indo-Malesian, *A. acuminatissima* (Bl.) Merr. & Perry; and one common to western Papua New Guinea and eastern Australia, *A. hemilampra* (F. Muell. ex F. M. Bailey) Merr. & Perry. At the time these studies were made, only a very few Papuan collections of *Acmena* were available (six were cited in the former paper and eight were cited in the latter); thus it is not surprising that now, with nearly eight times the number of collections at hand, we can see the need for some changes and additions.

We are of the opinion that three of the species Merrill and Perry recognized, *A. dielsii*, *A. laevifolia*, and *A. polyantha*, are more correctly placed in synonymy, and we recognize, among collections that have been made since their studies, three new species. In addition, we have found that the Papuan *Syzygium triphlebium* Diels, which was accepted in *Syzygium* by Hartley and Perry (1973), is more correctly placed in *Acmena*, and that *Syzygium acmenoides* Merr. & Perry, which was informally referred to *Acmena* by Hartley and Perry (1973: 220), is correctly placed in *Syzygium*. The purpose of this paper is to revise the Papuan species of *Acmena* in view of this new information.

As Merrill and Perry pointed out (1938), *Acmena* ranges from mainland Asia throughout Malesia to the Solomon Islands and south to northern and eastern Australia. We have restricted this study to the Papuan species because we believe it is advisable to study *Acmena* in conjunction with *Syzygium*, and our work on the latter genus, continuing that of Hartley and Perry (1973), is limited to that region. The Australian species of *Acmena* and *Syzygium* are being studied by B. P. M. Hyland, C.S.I.R.O. Division of Forest Research.

Specimens cited in this paper are deposited at the British Museum (Natural History), London (BM), the Queensland Herbarium, Brisbane (BRI), the C.S.I.R.O. Herbarium Australiense, Canberra (CANB), and the Rijksherbarium, Leiden (L). We wish to thank the directors and curators of these herbaria for making specimens in their care available to us. Thanks are also extended to the curator and staff of the Canberra Botanic Gardens for the opportunity to study living material of *Acmena smithii* (Poiret) Merr. & Perry.